ADAPTIVE CHANGES IN MORPHOLOGY AND BEHAVIOR OF *CLOSSIANA SELENE* LARVA (LEPIDOPTERA: NYMPHALIDAE)[1]

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ABSTRACT: The morphological and behavioral changes in the immature stages of *Clossiana selene*, a nymphalid found in Europe, are examined. A possible explanation for the adaptive significance of these changes is the varying array of predators and parasites which attack each instar.

The larvae of many lepidopterans undergo complex changes in morphology and behavior during development (Ford, 1945). Changes in color; number, size and pattern of hairs, spines and tubercles; and behavior such as the alarm response, occur as the instars progress. The present study investigates the possible adaptive significance of these changes in the larva of *Clossiana selene* Schiffermueller (Nymphalidae).

This butterfly occurs locally in woodlands, especially clearings, margins and damp areas, throughout most of Britain (South 1941). Its food plant is the violet, *Viola canina*. The first brood of adults emerges in June and July and eggs are laid within twelve days of emergence. There are five larval instars and each instar is morphologically distinct from any other. In Britain the majority of larvae enter hibernation during August as second, third, or fourth instars and begin feeding again the following April. The remainder feed up quickly after emerging from the egg, taking only twenty one or twenty two days to complete their larval development. Consequently they pupate and emerge as adults in the August of the same year. Matings from these individuals result in larvae which quickly grow to the third instar and hibernate before cold conditions ensue (Tutt, 1896; Frohawk, 1934).

The interruption of development by hibernation results in larval activity during two distinct seasons. More precisely, the first, second and third instars occur in summer from mid-June through August, (or August through September for the partial brood), while the majority of fourth and fifth instars are active in spring, mainly April through May. Instars occurring at different times of the year are likely to encounter different predators and parasitoids. In this paper I explore the possibility that changes in instar morphology and behavior can be explained in part by changes in kind and frequency of major larval enemies through time.

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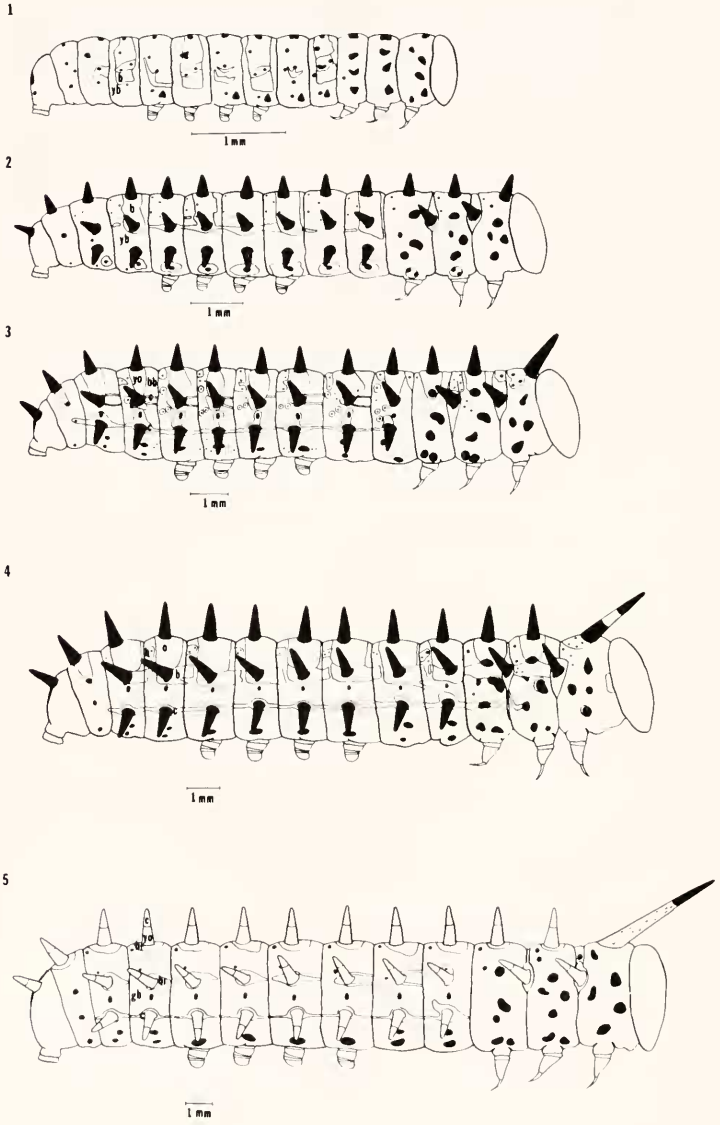

Fig. 1. Morphology of the five larval instars of *Clossiana selene*. The armature is drawn without hairs and spines. Symbols: b=black, yb=yellow-brown, yo=yellow ochre, bb=blue-brown, o=orange, br=brown, gb=grey-blue.

METHODS

One hundred and eight *Clossiana selene* larvae were kept in separate containers in well-shaded conditions similar to those found in their normal habitat. Each container was approximately twelve inches in height and consisted of a potted food plant with a closely fitting, ventilated plastic cover. Each larva remained in its container except for periods of study, and faeces were removed on alternate days. The plants were watered from the bottom. Records were kept on the morphology, especially the changes in size, armature (tubercles and spines) and color, and the behavior of each instar.

RESULTS

Morphology: The changes in morphology throughout the five instars of *Clossiana selene* are illustrated by Fig. 1. Changes occur between instars at ecdysis, and within each instar, once the coloration after ecdysis is complete, the only morphological feature to alter is the size. The first instar larva will grow from approximately 1.5 mm to 4.5 mm then ecdyse; the second instar increases to approximately 10 mm; and the third, fourth and fifth instar larvae increase in size to 14.5, 18, and 22 mm respectively before ecdysing.

The armature of the first instar is sparse and consists of tiny, fine hairs scattered over the surface and a few small clusters of fine spines protruding from shiny, black spots. Immediately upon ecdysis the black tubercles of the second instar larva are apparent, each bearing many spines projecting in diverse directions (see Fig. 2). Larger and more numerous hairs and spines are also present at this stage. Large tubercles and larger and more numerous spines feature in the third instar. The prothoracic tubercles are more prominent and extend to approximately one and a half times the length of the others. The tubercles have a size gradient with the largest ones situated dorsally and the smallest towards the ventral surface. The tubercles, hairs and spines are bigger in the fourth and fifth instars, corresponding to the increase in body size. Throughout, each large black spot usually bears two or three spines and each small dot has a single hair projecting from the center.

There is an overall increase in the number of spines over the body surface and on each tubercle between each instar, resulting in a densely coated fifth instar individual. By comparison the first instar individual appears naked.

The undersurface of every instar is dark grey-brown, mottled with lighter and darker areas, but the coloration of the dorsal surface varies with the instar. The first instar larva is mainly yellow-brown with some small black

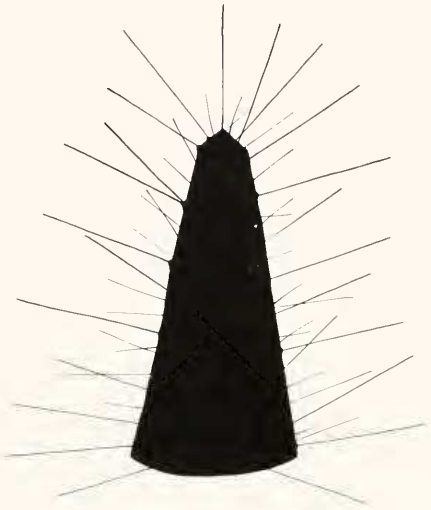

Fig. 2. A single tubercle from a fourth larval instar to show spines.

patches and several shiny black spots. The second instar resembles the first except for appearing generally darker because of the tubercles and more extensive black patches. The third instar is mainly dark blue-brown in color with lateral cream bands, dorsal yellow ochre pataches and some charcoal markings. The fourth (and first post hibernation) instar is lighter and brighter, being pale grey-blue with a lateral cream band, and the previously yellow ochre regions are now orange and more extensive. It also bears the prominent prothoracic tubercles which are differentiated into black and grey. The fifth instar appears as the brightest of all the stages being mainly dark grey-blue with lateral cream and brown bands and dark brown markings, and the general tubercles are differentiated into yellow ochre and cream. The spines remain black throughout the instars.

Behavior: The larvae feed mainly at night and generally on the undersurface of the leaves.

Defensive behavior of the first and second instar larvae differs from that of the third, fourth and fifth instars. In the former stages the larva is passive and any mechanical disturbance results in dislodgement from the leaf. However, in the latter stages the larva actively curls into a ball when disturbed and lies on its side with the head tucked in, protected by the last few abdominal segments, and the tubercles radiating in all directions. The larva often drops to the ground during this process.

DISCUSSION

The agents which reduce the numbers of the early instars of butterflies in general appear to be adverse weather conditions (heavy rain), fungal and viral diseases and parasites. The later stages and adults suffer from attack by parasites and invertebrate and vertebrate predators (Ford, 1945; Harcourt, 1966).

It is most probable that the principal selective force for particular color patterns is predation by vertebrates (especially birds in Britain) (Ford, 1945; Carpenter, 1937). Most of the nymphalid larvae have warning coloration, are armed with spines and are conspicuous on the food plant (Ford, 1945). In the case of *Clossiana selene*, the coloration and armature becomes well developed in the fourth and fifth instars and the earlier instars are generally much less conspicuous. The first, second and third instars, which are active predominantly mid-June through August, are small (less than 14.5 mm), moderately spiny and mainly a subdued yellow or blue-brown with black markings and spots. After hibernation the fourth and fifth instars are larger, eventually reaching 22 mm in length, have dense spines and large tubercles, especially on the prothorax, and exhibit bright colors with highly variable markings including orange and cream. While the background is dark grey-blue, the overall impression is bright therefore, the colors do not appear to be explicable in terms of thermoregulation, for example, the absorption of heat on emergence from hibernation.

The coloration and armature of the last two instars may be a response to heavy predation by birds. The appearance of most fourth and fifth instar larvae coincides with the breeding season of birds and the rearing of fledglings. While insect predation by birds can be very heavy at this season they are known to generally avoid hairy, conspicuous larvae and the coloration and armature of caterpillars are both important in deterring predators (Judd, 1899; Jones, 1932). The rolling behavior of the fourth and fifth instars when disturbed probably aids in repelling predators through the display of spines and tubercles.

Larvae avoid parasitoids by a variety of mechanisms including hiding, violent struggling when the parasitoid is near, falling from the food plant, the possession of a tough cuticle, or any combination of these (Askew, 1971). Since the early instars of *Clossiana selene* have relatively few and small spines and tubercles, and are relatively drabbly colored, their defense appears to be mainly by crypsis and catalepsis. It is these instars which may be the most vulnerable to parasitoids. Larvae and pupae of butterflies are parasitized by at least two major orders of insects, the Hymenoptera and the Diptera. Nothing is known of the specific parasites of *Clossiana selene* but the family

Nymphalidae is heavily parasitized by both orders (Thompson, 1944) and the incidence of parasitism is especially great during the early instars. The Tachinidae are the more generalized parasites and several species, for example, *Phryxe vulgaris*, attack close relatives of *Clossiana selene* (Audcent, 1942). It is very likely that patterns of parasite attack on *Clossiana selene* are very similar.

The available data and literature suggest that the changes in the morphology and behavior of the *Clossiana selene* instars is a response to changes in the relative frequency of its major enemies before pupation. The changes are perhaps exaggerated as a result of the larvae being active in two distinct seasons. Parasitoids are likely to be present at all times but the larvae are most vulnerable to them during the early instars. By contrast, predation by birds is likely to be at a maximum during the active period of the later instars which bear the largest spines and tubercles and which exhibit the brightest and most variable colors.

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REFERENCES

Askew, R.R. 1971. Parasitic insects. New York: American Elsevier.

Audcent, H. 1942. A preliminary list of the hosts of some British Tachinidae (Dipt). Trans. Soc. Brit. Ent. 8:1-42.

Carpenter, G.D.H. 1921. Experiments on the relative edibility of insects with special reference to their coloration. Ent. Soc. Lond. Trans. 69:1-105.

Ford, E.B. 1945. Butterflies – London: Collins.

Frohawk, F.W. 1934. The Complete Book of British Butterflies London: Ward, Lock.

Harcourt, D.G. 1966. Major factors in survival of the immature stages of *Pieris rapae* (L.). Can. Entomol. 98:653-662.

Jones, F.M. 1932. Insect coloration and the relative acceptability of insects to birds. Ent. Soc. Lond. Trans. 80:345-385.

Judd, S.D. 1899. The efficiency of some protective adaptations in securing insects from birds. Amer. Nat. 33:461-484.

South, R. 1941. The Butterflies of the British Isles. London: Frederick Warne.

Thompson, W.R. 1944. A Catalogue of the Parasites and Predators of Insect Pests. Part 5. The Imperial Parasite Service, Belleville, Ontario, Canada.

Tutt, J.W. 1896. British Butterflies. London.